

Modeling Global Macroclimatic Constraints on Ectotherm Energy Budgets¹

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SYNOPSIS. We describe a mechanistic individual-based model of how global macroclimatic constraints affect the energy budgets of ectothermic animals. The model uses macroclimatic and biophysical characters of the habitat and organism and tenets of heat transfer theory to calculate hourly temperature availabilities over a year. Data on the temperature dependence of activity rate, metabolism, food consumption and food processing capacity are used to estimate the net rate of resource assimilation which is then integrated over time. We detail and explore the significance of assumptions used in these calculations.

We present a new test of this model in which we show that the predicted energy budget sizes for 11 populations of the lizard *Sceloporus undulatus* are in close agreement with observed results from previous field studies. This demonstrates that model tests are feasible and the results are reasonable. Further, since the model represents an upper bound to the size of the energy budget, observed residual deviations form explicit predictions about the effects of environmental constraints on the bioenergetics of the study lizards within each site that may be tested by future field and laboratory studies.

Three major new improvements to our modeling are discussed. We present a means to estimate microclimate thermal heterogeneity more realistically and include its effects on field rates of individual activity and food consumption. Second, we describe an improved model of digestive function involving batch processing of consumed food. Third, we show how optimality methods (specifically the methods of stochastic dynamic programming) may be included to model the fitness consequences of energy allocation decisions subject to food consumption and processing constraints which are predicted from the microclimate and physiological modeling.

Individual-based models that incorporate macroclimatic constraints on individual resource acquisition, assimilation and allocation can provide insights into theoretical investigations about the evolution of life histories in variable environments as well as provide explicit predictions about individual, population and community level responses to global climate change.

INTRODUCTION

Impending global climate change will undoubtedly make the world less hospitable to some species of organisms and more hospitable to others. This realization has stimulated considerable interest in understanding how organisms respond to their changing environments and how these responses affect population size and dynamics. If we understand the mechanisms of interaction between environments and individuals, we can use individual-based models to predict the emergent properties (*sensu* Salt, 1979) of populations of interacting individuals and thereby model population level responses

to specific environmental changes (Huston *et al.*, 1988). Further, as changes in age structure and/or population size occur, we can also assess potentially destabilizing community-wide effects among other populations whose dynamics are ecologically interrelated.

Predicting the outcomes of various scenarios of climate change on populations of interacting individuals has traditionally been viewed as an applied area of ecology. However, understanding the links between environments and individuals is of great theoretical significance as well. Recently, several reviews have emphasized that investigations of the mechanisms of individual response belong in the realm of more general questions about the evolution of life histories in variable environments (Congdon *et al.*, 1982; Dunham and Miles, 1985; Dunham *et al.*, 1988a, 1989; Congdon, 1989; Wilbur and Morin, 1988). A general approach to the question of how to model

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population response to climate change is to emphasize that selection acts on the responses of individuals to their environments and ask how changing environmental constraints influence the expression of life history characters and the evolution of life history strategies. According to Dunham *et al.* (1989), the problem is to define the set of driving processes at the individual level which affect birth, death, emigration and immigration rates which are the system state variables and then predict the population size at the next time interval (see also Huston *et al.*, 1988). The set of responses, in what Dunham *et al.* (1989) refer to as a "time-ordered sequence of age-specific allocation decisions," by individuals determines these state variables and is characteristic of the life history phenotype. Given any set of fixed or stochastically varying environmental constraints, and given the physiological state of the organism (which has resulted from past constraints and allocation decisions), the life history strategy transduces energy and mass into progeny. Heritable variation in phenotypic response, *i.e.*, life history strategy, that results in relatively greater ability to survive and reproduce will be selected (see Congdon, 1989; Dunham *et al.*, 1989). Therefore, the applied issue of modeling population responses to climate change is in fact a special case of the general problem of modeling life history evolution in variable environments.

Our aims in this paper are to describe how we model global macroclimatic constraints on animal energy budgets, to address the implications and limitations of the assumptions of our current modeling formulations, and to outline necessary data and techniques for more advanced models. We present a simple mechanistic model that establishes bounds to the problem of predicting animal responses to variable environments for the case of small ectotherms (see Porter, 1989, for a discussion of energy budgets for endotherms and larger ectotherms). We also examine concordance between model predictions and observed geographical variation in life history characters among 11 populations of *Sceloporus undulatus* to demonstrate that model tests are feasible and the results are reasonable. A compari-

son such as this is relevant for predicting the effects of climate change on the life histories of small ectotherms since the magnitude of variation in environmental characters among sites differing in elevation by a few hundred meters or a few degrees in latitude is on the order of predicted variation according to many scenarios of global climate change (COHMAP, 1988).

An important goal of this paper is to make macroclimatic constraint/energy budget models more accessible to researchers in a wide variety of areas not presently involved with this type of modeling, and to provide sufficient direction for interested readers to construct their own versions of these models. Additionally, we highlight the areas where our models are deficient and provide directions and guidelines for making specific improvements tailored for use in other specialized implementations of the general questions we pose.

Figure 1 provides a summary schematic of our modeling efforts and illustrates the major areas of emphasis in this paper to be detailed in the next section (Current Modeling Formulation). The first step is to model the mechanistic links between an animal and its environment and establish the constraints that operate on its life history phenotype. Any environmental factor that elicits or constrains individual phenotypic responses and thereby affects birth and/or death processes is defined as operative and should be included (Spomer, 1973; Dunham *et al.*, 1989). In this figure, we focus on modeling time constraints from the thermal biophysical environment on resource acquisition, assimilation and allocation; however, we suggest that including the effects of the resource, predation and social/demographic environments is essential to modeling the complete system dynamics (see Dunham *et al.*, 1989, for a more complete system diagram).

The upper portion of Figure 1 indicates that macroclimatic input parameters (such as global solar radiation and local parameters specific to the habitat of interest such as substrate type and topography) are combined with organism biophysical and physiological properties to determine the distribution of available thermal microclimates

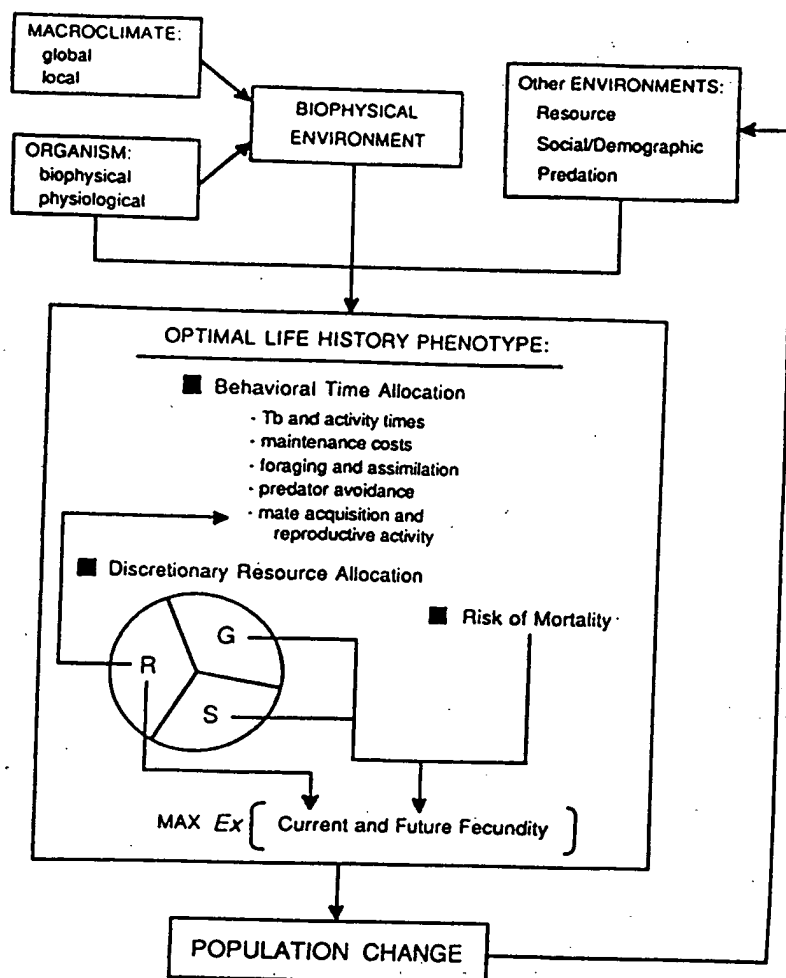


FIG. 1. Summary schematic showing the mechanistic links between an ectotherm and its environment which establish the operative constraints on the optimal life history phenotype. See text for explanation.

(methods described below). This distribution is defined as the operative biophysical environment, and all activities (such as thermoregulation, foraging, digestion, mate acquisition and predation) and inactivity are constrained to occur within this distribution (Grant and Dunham, 1988; Grant, 1990).

The pattern of behavioral time allocation determines the daily accumulation of resources (energy, water and nutrients) as well as the daily resource expenditure due to maintenance and activity. Body temperatures and activity times result from (a) tradeoffs among these resource gains and losses, (b) performance constraints stem-

ing from temperature-dependent capacities to digest food, locomote, and perform other vital functions (Huey, 1982), and (c) the constraint that thermally suitable microclimates are available in sufficient frequency in the ectotherm's home range for activity to occur (Christian *et al.*, 1983; Waldschmidt and Tracy, 1983; Grant and Dunham, 1988, 1990; Grant, 1990).

We define the total amount of assimilated resource available for allocation to growth (G), storage (S) or reproduction (R) over some "biologically meaningful time period" (Congdon *et al.*, 1982) in a life history as the discretionary resource. This amount is

similar to the "production budget" in Congdon *et al.* (1982) except that we advocate the inclusion of reproductive activity expenditure in the fraction, R , that is allocated to reproduction. This inclusion is a necessary step in order to formulate individual reproductive effort according to Fisher (1930; see also Hirshfield and Tinkle, 1975). In addition, for any temporal pattern of activity and T_b selection, and for any allocation pattern of assimilated resource into G , S , and R , there will be a combined associated risk of mortality for any individual time and resource allocation phenotype (Dunham *et al.*, 1989). This combined risk will be the product of all independent risks associated with each time or resource allocation "decision."

The allocation of the discretionary resource among the competing categories of growth, storage and reproduction is a behavioral optimization problem and is hypothesized to maximize the expected sum of current and future fecundity (Williams, 1966; Hirshfield and Tinkle, 1975). For stochastic or probabilistic environments, the problem of constrained optimization of resource allocation can be approached using standard optimization procedures (*e.g.*, King and Roughgarden, 1982; Sibly *et al.*, 1985; Hom, 1988; Hom *et al.*, 1990; Mangel and Clark, 1988; Taylor and Gabriel, 1992).

Behavioral and physiological "choices" affecting the expected age-specific survival and fecundity of individual life history phenotypes will determine population level shifts in age- and size-structure, generation time, population size and growth rate, and other emergent characteristics (Salt, 1979; Huston *et al.*, 1988). These in turn will influence the constraints that operate on the optimal life history phenotype stemming from "Other Environments" in Figure 1, *e.g.*, by affecting the intensity of resource or mate competition or predation risk (Dunham *et al.*, 1989).

CURRENT MODELING FORMULATION

This section provides a brief overview of the methods we have developed to simulate operative environmental temperature, T_e , availability and concomitant constraints on the body temperatures, times of activity,

and energy budgets of a typical ectotherm—a small rock dwelling lizard (see Porter, 1989, for endotherms and larger ectotherms). The most accurate method to assess T_e availability and activity constraints is to measure these directly (*e.g.*, Grant, 1990; Grant and Dunham, 1990). However, these methods are not useful in examining thermal constraints imposed by environments in the past or by hypothetical future environments under various scenarios of climate change. Our objective is to bound the problem within the narrowest possible limits (Porter, 1989). This simulation proceeds in three parts: (A) delineate the physical microclimate characters for a hypothetical perching location, (B) calculate the operative environmental temperature, T_e , for a lizard with specified surface heat transfer properties, body posture and solar orientation, and (C) estimate the resource ingestion and assimilation rate from regressions derived in lab as a function of body temperature, T_b .

Figure 2 illustrates the topographic complexity and concomitant thermal heterogeneity of real environments (upper panel) which should be compared with the abstracted version of this environment required by this simulation (lower panel). This schematic illustrates what is needed to solve the energy balance equation for the substrate and for the hypothetical lizard. Simplifying assumptions in the microclimate simulation are adequate to reduce the complexity of the real environment into a small number of characteristic parameters and mechanisms of heat flux according to basic transient heat transfer theory (see also Kreith, 1973; Porter, 1989). Figure 3 illustrates the energy balance equation which is used both for microclimate and ectotherm temperature simulations with only minor modifications (see Porter *et al.*, 1973, for an expanded and detailed treatment of these equations). For example, for the substrate, the diagonal heat balance equation simply excludes the term for metabolism, and for points below the substrate surface, all terms in the diagonal equation would be equal to zero except for conduction and storage of heat. The resulting simulated biophysical environment includes the range of available

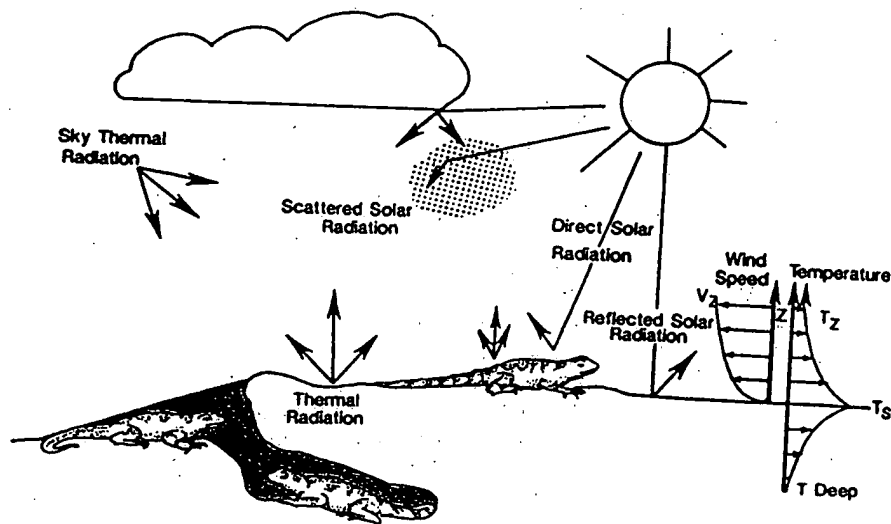


FIG. 2. UPPER PANEL: Photo of a typical lowland rocky desert habitat, near Boquillas, Texas, where *Sceloporus merriami* are abundant. This illustrates the topographic complexity and concomitant thermal heterogeneity of real environments available to thermoregulating lizards. LOWER PANEL: Schematic representation of the thermal environment showing the relevant heat fluxes and other factors needed to solve the energy balance equation for the substrate and for the hypothetical lizard. The location of lizards illustrates the three perch microclimate conditions used by the simulation described in this paper.

surface temperatures for activity as well as the temperature of inactive lizards in deep caves. This will sufficiently bound the problem by placing upper and lower limits on activity time, resource acquisition and assimilation.

Physical microclimate simulation

Real lizards can be active on horizontal or sloping rock surfaces and exposed to direct and/or indirect sunlight, partial shade, or deep shade exposed to the sky; alternatively, the lizard may cease activity and retreat into

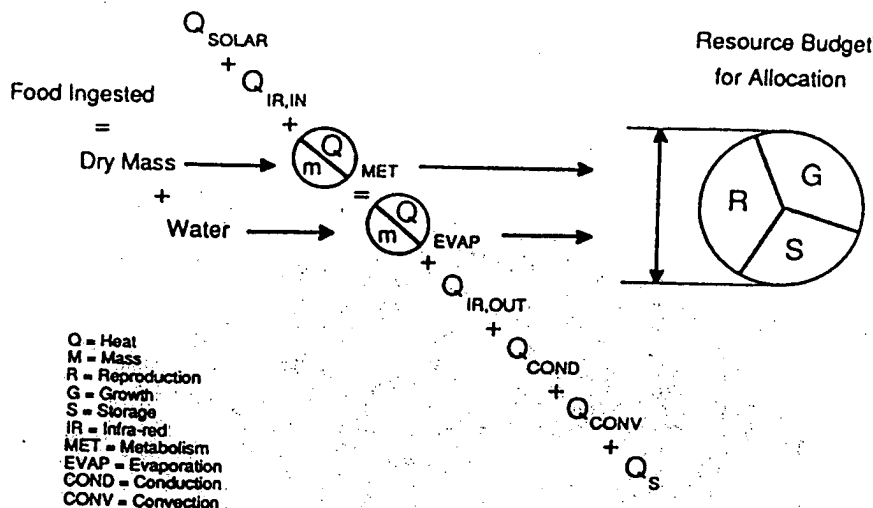


FIG. 3. Overview of the coupled equations for the heat balance, along the diagonal, and for the mass balances along the horizontal for a typical ectotherm (see Porter, 1989, for a more detailed treatment). Food ingested (at left) is processed and then available for allocation to growth (G), storage (S), or reproduction (R) in an ecological energy and water budget (at right).

caves and crevices to find T_s anywhere between the air temperature at 2 meters and the temperature in deep caves (Porter *et al.*, 1973; Porter, 1989). However, this model only considers the bounding values of available T_s by simulating perch microclimate conditions in one of three extremes—a horizontal perch, a perch in full shade but exposed to the sky, or a perch in a deep cave (Fig. 2, lower panel).

The simulation proceeds by specifying physical characters of the locality to be modeled such as elevation, site slope angle, substrate solar absorptivity, conductivity, and surface roughness (see Porter, 1989, for representative values). Maximum and minimum air temperatures (T_a) and wind speeds (V) at reference height (2 m), as well as the time of day when these extremes occur, are obtained from standard climate data sets for a particular date of interest. These inputs are fit to sinusoidal curves to obtain hourly estimates of $T_a(t, 2 \text{ m})$ and $V(t, 2 \text{ m})$. The surface roughness parameter is used with the $V(t, 2 \text{ m})$ curve to fit a logarithmic function to estimate the wind speed $V(t, z)$ as a function of height (z) and time (t) (Porter *et al.*, 1973). To obtain $T_s(t, z)$ the simulation assumes the deep cave temperature is fixed

at mean monthly temperature and estimates the surface temperature based on numerically solving a version of the heat balance equation (Fig. 3) for the substrate and points below. This solution relies on a subroutine (SOLRAD, McCullough and Porter, 1971) to calculate the incident diffuse and direct global solar radiation load for the particular perch slope and azimuth angles.

With the reference height and deep cave temperatures known, the simulation uses a finite difference heat transfer algorithm (Adams Predictor-Corrector numerical integrator, G.E.A.R. package, Argonne Laboratories) to find the surface and intermediate temperatures between the reference height and deep soil temperatures, $T_s(t, z)$ and $T_d(t, z)$. This simulation must be repeated for each of the two exposed perches (horizontal perch and a perch in shade) for which the $T_s(t, z)$ curve for the latter is calculated with the direct component of solar radiation from SOLRAD set to zero. With the microclimatic conditions of radiation, temperature, and wind speed calculated for the hypothetical perches, we are ready to place an hypothetical lizard in these perches and estimate the operative environmental temperature, T_e .

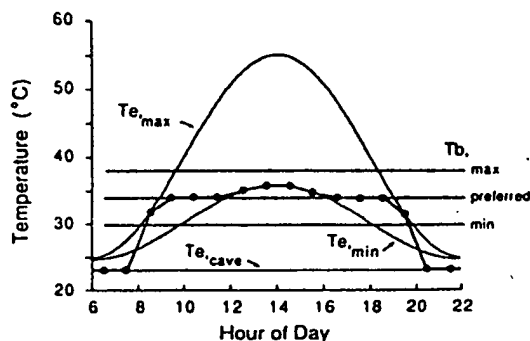


FIG. 4. The predicted range of environmental temperatures ($T_{e,max}$, $T_{e,min}$, and $T_{e,cave}$) available to active and inactive lizards for each hour of the day. Lizard activity is assumed to occur if either of the exposed microclimate T_e s are within the user-defined range of $T_{b,max}$ and $T_{b,min}$. During activity the lizard is assumed to regulate its T_b (solid points) as close as possible to the $T_{b,pref}$ (see text for method of estimation). During inactivity, the lizard's T_b equals the $T_{e,cave}$.

Ectotherm operative environmental temperature simulation

Surface heat-transfer properties and temperature dependent metabolic and water loss rates of the lizard of interest are used in combination with the driving microclimatic conditions to solve the diagonal heat balance equation in Figure 3. This calculation is repeated at hourly intervals for each of the three perches in (A) which will delineate the range of available T_e s to active and inactive lizards (Fig. 4). Since the exposed horizontal perch represents the maximal T_e available, the lizard is assumed to maintain the greatest possible fraction of its body surface exposed to sunlight throughout the day. Body orientation is assumed to have no effect on the T_e s for the exposed shaded and deep cave perches since there is no direct sunlight. The T_e for the deep cave perch, which will be used during inactivity, is assumed to equal the deep cave temperature.

Upper and lower acceptable bounds for body temperature, T_b , during activity are input for the lizard of interest, and for each hour of the day the lizard will be inactive if both exposed $T_e(t)$ s are outside the range of acceptable T_b (both too hot or both too cold), otherwise the lizard is active (see Fig. 4). With bounds set for both the length of

time and for the range of body temperatures during activity, we are ready to allow the hypothetical lizard to attempt to select its physiologically optimal body temperature and consume and digest food resources.

Ectotherm physiological simulation

Laboratory determined temperature-dependent metabolic rate, food consumption and digestive processing rate are used in combination with activity and T_b estimates from (B) to estimate the total amount of energy (less maintenance and digestive costs) ingested and assimilated by the lizard. Resting metabolic rates for this simulation are obtained from a regression in Bennett and Dawson (1976; see Appendix A). Although this equation was calculated from a wide variety of lizards and represented an important early contribution to studies of physiological allometry, the predicted value as a function of T_b and body size might differ considerably from the actual measured value for the particular lizard of interest due to a wide variety of important ecological and evolutionary considerations (Bennett and Dawson, 1976; McNab, 1979; Nagy, 1982). Ideally, the equation relating metabolic rate to T_b and body size should be estimated from data on individuals from the specific population and possibly also season of interest. The metabolic rate of an active lizard is assumed to be a constant fraction times the resting rate (=activity scope, Bennett and Dawson, 1976; Congdon *et al.*, 1982; see Appendix A).

Maximal food consumption and assimilation rates were determined for a lizard as a function of T_b by estimating the steady state rates of ingestion and excretion (J/day) by lizards held at constant cage temperature in an ad lib feeding regime (data from *Sceloporus undulatus*, Waldschmidt, 1984; Waldschmidt *et al.*, 1987). Consumption and assimilation rates were fit to polynomial regressions, and the energetic cost of digestion (referred to as the specific dynamic action) was estimated in lab as a function of T_b (see Appendices A and B). To simulate the consumption and assimilation rates for the hypothetical lizard, it is assumed that these rates for an hour of activity at a given T_b equal $1/24$ of the laboratory estimated daily

rates at that T_b . This is equivalent to assuming that these lizards are entirely "process limited" (Congdon, 1989), i.e., their energy budgets are not constrained by their ingestion rate, but rather by their digestion and assimilation rate. Such an assumption would represent an upper bound on the amount of energy consumed. However, since this assumption may not hold for lowland desert environments (e.g., Dunham, 1981; Congdon, 1989), the simulation allows for ingestion limitations by simply taking a constant fraction of the maximal ingestion rate obtained from the ad lib feeding regime such as 75% or 50% of maximal food consumption capacity.

Perhaps a more significant assumption of the present physiological model is that no feeding is allowed to occur when the animal is inactive, and thus no digestion and assimilation can occur either. The fraction of food eaten during any particular hour of activity is assumed to be assimilated during that hour according to the regression for assimilation rate as a $f(T_b)$. In other words, regardless of what T_b the lizard exhibits in subsequent time intervals during which digestion would normally occur in real lizards, the mass budget of the hypothetical lizard is credited with digesting the consumed food, and debited the energetic cost of digesting that food, depending on its T_b during the time interval of consumption, i.e., assimilation is instantaneous. This could represent an upper bound to the processing capacity of the lizard, since in many situations the temperature during inactivity (overnight or at midday) is lower and assimilation rate would be greatly reduced (see Appendix A). On the other hand, this model could underestimate food processing capacity for lizards that feed in cool microclimates such as in early morning (e.g., desert sceloporines) or underwater (e.g., marine iguanas) and have access to warmer microclimates later in the day in which to digest their food at a thermally enhanced processing rate. This assumption is a current focus of concern and in a later section we describe how to allow for batch processing of ingested resource in which the lizard may digest and assimilate food during time intervals subsequent to consumption as a function of its

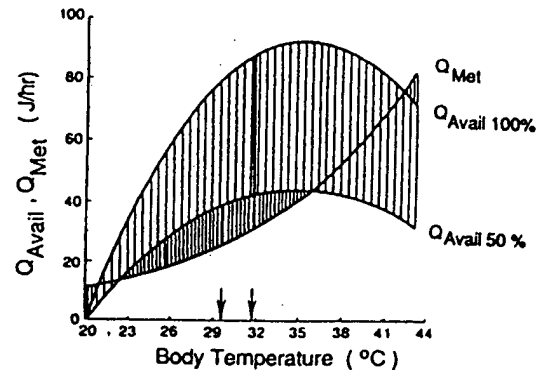


FIG. 5. Sample output from the physiological model for a 5 g *Sceloporus undulatus* describing the temperature dependence of resource intake, processing, and expenditure (in J/hr, equations in Appendix A). $Q_{AVAIL, 100\%}$ and $Q_{AVAIL, 50\%}$ represent the total assimilated energy for 100% and 50% of *ad lib.* feeding, respectively. Q_{MET} is the total metabolic expenditure for an activity scope of 1.5 times resting. The difference between Q_{MET} and either Q_{AVAIL} is the net amount of assimilated energy available for allocation in the energy budget. Arrows indicate the T_b at which net assimilated energy is maximal for each feeding regime, and the model uses this temperature as the preferred temperature during activity by the hypothetical lizard (see Fig. 4).

T_b at these later times. Batch processing models represent an important step in incorporating thermal constraints on transient resource processing capacity (see below).

Figure 5 is a sample output from the physiological model for a 5 g *Sceloporus undulatus* and describes the temperature dependence of resource intake and expenditure (J/hr, equations in Appendix A). The convex decelerating curves represent the total assimilated energy (consumption \cdot fraction assimilated) for unlimited food and for a reduced food level to 50% of *ad lib.*, ($Q_{AVAIL, 100\%}$ and $Q_{AVAIL, 50\%}$, respectively). The exponentially increasing curve is the metabolic expenditure, Q_{MET} , for an activity scope of 1.5 times resting. The difference between the Q_{MET} and either of the total assimilation curves represents the net amount of assimilated energy available for discretionary allocation to growth, storage, or reproduction for either of the feeding regimes. As can be seen, these data indicate that an hypothetical reduction in available food from *ad lib.* conditions to only 50% of

ad lib. food consumption greatly reduces discretionary energy at any body temperature. Note that at temperatures above about 36°C for the 50% *ad lib.* regime, the lizard would be in a negative energy balance. During activity, the hypothetical lizard is assumed to have access to an intermediate thermal microclimate in which it may be active at the T_b which maximizes its net energy discretionary energy intake per hour (see " $T_{b,preferred}$ " in Fig. 4, and the arrows in Fig. 5). Note in Figure 5 that this temperature is lower when the lizard has limited access to food than when food is unlimited. This model is consistent with results from other ectotherms such as freshwater fishes (Brett, 1971; Magnuson and Beiting, 1978; Crowder and Magnuson, 1983) and aquatic insects (Vannote and Sweeney, 1980), but has yet to be tested in lizards.

MODEL PREDICTIONS

Development and testing of the microclimate and steady-state ectotherm temperature simulations have been ongoing for the past two decades. These studies have shown how coupled daily and seasonal biophysical constraints on activity time and resource acquisition and processing capacities affect (a) individual daily thermoregulatory behavior (Beckman *et al.*, 1973; Porter *et al.*, 1973), (b) seasonal potential for growth, storage and reproduction (Porter and James, 1979; James and Porter, 1979; Porter and Tracy, 1983; Porter, 1989), (c) species distribution limits (Porter and Tracy, 1983), and (d) trophic interactions among species (Porter *et al.*, 1975). In this section, we present an additional test of this modeling in which we compare observed and predicted integrated annual energy budget sizes for *Sceloporus undulatus*, which is one of the most well-studied lizards in North America.

The extensive geographic range of *S. undulatus* (from Florida to New Jersey, west to Utah, and south into north-central Mexico) as well as their highly variable life history characters among populations (see reviews in Tinkle and Dunham, 1986; Dunham *et al.*, 1988a) render this lizard ideal for modeling macroclimatic constraints along environmental gradients. According to extensive analyses by Tinkle and Dun-

ham (1986) and Dunham *et al.* (1988a) using data from 11 populations throughout this range, very little of the observed life history variation can be explained by any simple hypothesis (due either to absence of pattern or absence of data). In particular, these authors could find no evidence to support the suggestion by Ferguson *et al.* (1980) and Ballinger *et al.* (1981) that life history characters should show convergence in similar environmental types, which suggests that environmental constraints on these lizards exert little if any effect. However, this could easily have been due to the coarseness of the initial environmental classification system (Tinkle and Dunham, 1986), which relied heavily on structural differences among habitats and would necessarily only provide a crude estimate of the daily and seasonal thermal environmental constraints impinging on these lizards. Direct estimates of variation in temperature availability are necessary to delineate macroclimatic constraints on daily and seasonal activity time and concomitant resource accumulation and allocation in a life history (Grant and Dunham, 1988, 1990).

The macroclimatic constraint/energy budget model we presented in the previous section provides a greatly improved test of the hypothesis that environmental factors affect variation in life historical energy budgets among populations of *S. undulatus*. Table 1 summarizes available life history data that we used to estimate differences in annual reproductive output among 10 populations compiled by Dunham *et al.* (1988a) and one population in New Jersey (P. Niewiarowski, personal communication). If annual net storage were near zero (which would be the case if lipids cycled but showed no annual accumulation), and if growth were near zero (which is reasonable for reproductively active adult lizards, Andrews, 1982), then this estimate of the annual mass allocation to reproduction for each site may be quite similar to the total annual energy budget size which is the final output prediction of our model.

To drive the microclimate and ectotherm models for each of the 11 study sites, we used long term average air temperatures from nearby weather stations, we estimated

local substrate physical characteristics from the descriptions in the respective sources, and we used biophysical and physiological data on *Sceloporus undulatus* as described above (see Appendices A and B). Additionally, since body size greatly affects stomach capacity, food consumption and processing rate (Appendix A), we used the observed average snout-vent lengths of adult females for each site for these simulations. Lastly, it should be noted that we assumed, due to an absence of evidence, that these biophysical and physiological characters for *S. undulatus* do not differ among seasons and sites (we return to this assumption below).

Figure 6 shows the observed annual total dry wt of eggs vs. the predicted maximum annual mass available for allocation to eggs according to our simulation. Note that none of the observed values greatly exceed the maximum predicted values for each site which shows that the model does not underestimate the upper bound for any of these sites. Secondly, note that there is a significant polynomial regression of observed annual reproductive output, Y , on predicted annual energy budget size, X ($Y = -1.20 + 1.87 \cdot X - 0.17 \cdot X^2$, $R^2 = 0.842$, $n = 11$, $P < 0.01$). Given the large number of assumptions required to generate the predicted values, as well as the diverse and often crude field methods used to estimate the observed reproductive parameters (especially clutch frequency), some may find it remarkable that any relation exists at all, let alone one that explains this much of the variance.

The comparison in Figure 6 suggests that environmental constraints among these sites do operate on daily and seasonal activity time and thereby exert an effect on observed annual reproductive output. This is broadly consistent with the earlier suggestion (see above) that similar life histories, at least with respect to total production budget sizes, may result in similar environments. However, this model can make no predictions about how this resource should be allocated in terms of egg size, clutch size, and the number of clutches per year—all of which vary greatly among sites (Table 1) and are basic characters of a life history (Dunham *et al.*, 1989). Our result only suggests that the total

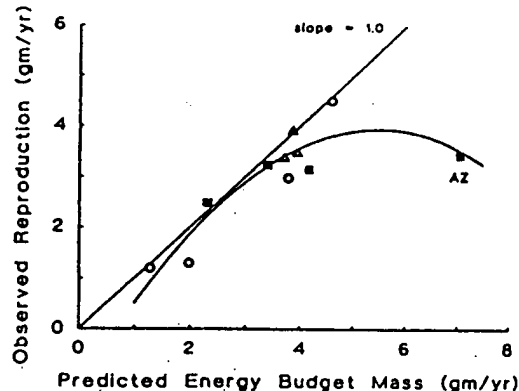


FIG. 6. Observed annual reproductive output (g dry wt) vs. predicted annual energy budget size (g dry wt) for 11 populations of *Sceloporus undulatus* from throughout their geographic range. The "observed" data and habitat classes for all sites except New Jersey were summarized in Dunham *et al.* (1988a, see Table 1). Data from New Jersey are from ongoing work by P. Niewiarowski (personal communication). Squares are from canyonlands (left to right—Pinos Altos [New Mexico], Utah, Colorado, and Arizona), circles are from grasslands (left to right—Nebraska, Kansas, Texas and Lordsburg [New Mexico]), and triangles are from woodland sites (top to bottom—Ohio, South Carolina and New Jersey). A reference line appears with slope 1.0 and intercept 0. The polynomial regression (Observed = $-1.20 + 1.87 \cdot \text{Predicted} - 0.17 \cdot \text{Predicted}^2$, $R^2 = 0.842$) is based upon data from all 11 sites.

amount of resource available for allocation is constrained, which may provide insights into allocation rules when combined with other modes of inquiry (see Dunham *et al.*; 1988b).

An important function of broad comparisons such as in Figure 6 is to direct future efforts by suggesting specific hypotheses to be tested by experiments (Dunham *et al.*, 1988b, 1989). For example, several hypotheses may be posed to explain why some of the observed values are much less than the maximum predicted and why the regression is a non-linear function. First, the model assumes that all of these lizards are limited by their capacity to process food with no limitations on ingestion rate (see Congdon, 1989); consequently, greater annual accumulation is predicted in warmer environments with higher processing rate and longer integrated annual activity time. However, if the observed warmer environments also tend to have lower availabilities

TABLE 1. Summary of available life history data on *Sceloporus undulatus* used to estimate observed geographic variation in annual reproductive output.

Study site	Habitat type	Clutch size	Clutches per year	Egg wet mass (gm)	Adult ♀ SVL	Weather data from
Arizona ^a	C	8.3	3	0.29	65	Phoenix, AZ
Utah ^b	C	6.3	3	0.36	69	Cedar City, UT
Colorado ^c	C	7.9	2	0.42	70	Grand Junction, CO
Pinos Altos, NM ^d	C	7.2	2-3	0.29	63	Beaverhead, NM
Lordsburg, NM ^d	G	9.9	4	0.24	68	Lordsburg, NM
Kansas ^e	G	7.0	1-2	0.26	57	Topeka, KS
Nebraska ^f	G	5.5	2	0.23	55	North Platte, NE
Texas ^g	G	9.5	3	0.22	57	San Angelo, TX
Ohio ^h	W	11.8	2	0.35	75	Lancaster, OH
South Carolina ⁱ	W	7.4	3	0.33	63	Aiken, SC
New Jersey ^j	W	9.0	2	0.395	73	Pemberton, NJ

^a Modified from Dunham *et al.*, 1988a. Sources: ^a Tinkle and Dunham (1986). ^b Tinkle (1972). ^c Tinkle and Ballinger (1972). ^d Vinegar (1975a, b). ^e Ferguson *et al.* (1980). ^f Ballinger *et al.* (1981). ^g P. Niewiarowski (personal communication). Habitat types are C—canyonlands, G—grasslands, W—woodlands. Weather data were obtained from the U.S. Climatological database for the recording station nearest and most similar in elevation to the exact location of each study site. Annual reproductive output was calculated as clutch size · clutches/yr · egg wet mass, for which we used values of 1.5, and 2.5 for clutches/yr of "1-2" and "2-3", respectively. We used data in Vitt (1978) to convert to dry weight for comparison with the model prediction (dry weight [g] = 0.4743 · wet weight [g]).

of food (such as may occur in desert grasslands or canyonlands), then the observed values for energy budgets in these habitats will be much less than predicted, whereas in cooler food-rich environments (such as northern and montane grasslands, or woodlands) observed and predicted values are expected to be much closer. These effects could lead to increased deviation of the observed reproductive output from the predicted maximal energy budget size as the latter increases. In fact, the regression after omitting the warmest and driest site, Arizona, is highly linear ($Y = -0.052 + 0.912 \cdot X$, $R^2 = 0.868$, $P < 0.0001$) with a slope not different from 1.0 ($t = 0.70$, $df = 8$, $P > 0.05$). This suggests that the energy budgets of *S. undulatus* are limited by food ingestion rate at the Arizona locality, whereas, at the other sites, budgets are limited by food processing capacity (see also Congdon, 1989). These results clearly point to the need to estimate food availability in field studies of life history variation (e.g., Dunham, 1978), and to conduct resource manipulation experiments to determine in which environments do increases in food availability actually lead to increases in the amount of resource available for allocation (e.g., Waldschmidt, 1983; Guyer, 1988a, b; Grant and Contreras-Arquieta, unpublished data).

There are several other hypotheses that can account for the non-linear regression in Figure 6, all of which underscore the need to incorporate other types of inquiries in developing and testing energy budget models. For example, since warmer environments may also be drier, such as in deserts, and since about 50% of the mass of freshly oviposited *Sceloporus undulatus* eggs is due to water (Vitt, 1978), water may limit annual reproductive output more so than does energy in warm and dry environments. In other words, even if a desert lizard has sufficient energy to produce an additional egg, unless she also has the minimal water store to hydrate that egg she will have to allocate that energy elsewhere in her life history (e.g., to growth or storage). Modeling this scenario requires a coupled simulation of the annual water and energy budgets of the study lizards (we thank A. E. Dunham for this intriguing suggestion).

Another explanation for the non-linear regression in Figure 6 is if there were a lower fractional allocation to reproduction at larger total energy budget size. This could result from a constraint on maximal egg production rate at larger potential production budget sizes (e.g., if the rate of yolking a clutch were limiting, or if egg development or post-hatching growth rates were low and ovipositions were constrained to occur early in

the breeding season to insure juvenile survivorship). On the other hand, if demographic characters were such that low adult body sizes and high reproductive output were selected (e.g., high adult mortality and early age of maturity), concomitant total energy budget sizes would be low and the fraction allocated to reproduction could be high (discussed in Tinkle and Dunham, 1986; Dunham *et al.*, 1988a).

Some of the residual variation in Figure 6 no doubt results from several basic sources some of which are peculiar to the model. For example, a problem with this simulation is that the driving environmental macroclimatic data were not available from any of the study sites either because these data were not collected or not reported. Typically, the data that were available were from nearby airports (see Table 1), the biophysical environments of which may poorly reflect those available to lizards on their rocky and/or coarsely vegetated home ranges. Another potential source of variation is that the model assumes clear skies throughout the year and undoubtedly the study sites differ in annual cloud cover. Cloud cover generally reduces environmental temperatures which could decrease total energy budget size if these cooler temperatures inhibit activity, foraging and digestion; on the other hand, cloud cover could have the opposite effect on activity, food consumption, and energy budget sizes if sunny conditions are thermally stressful, such as during southern and low elevation summer days. We strongly suggest, as have others (Waldschmidt and Tracy, 1983; Tracy and Christian, 1986; Dunham *et al.*, 1989; Grant and Dunham, 1990), that studies of ectotherm population biology include detailed estimates of the thermal environments available to and used by the study individuals.

Another potential source of error in the model stems from the assumption of identical thermal physiologies for the 11 *S. undulatus* populations modeled. What little data are available on activity T_b suggest the opposite may be true. For example, *S. undulatus* exhibit different average active T_b s in New Jersey than they do in Nebraska by several °C, and the effect of this on their

activity and seasonal energy budgets may be great (P. Niewiarowski and W. Roosenberg, unpublished data). However, comparable field data are unavailable from other sites, and even simple comparisons under laboratory conditions are lacking to support or reject the use of the same metabolic and food processing capacity equations among all sites and seasons (Appendix A). Seasonal acclimation of physiology is well known for lizards (e.g., Nagy, 1982), and when the generating physiological regressions are known for each population and season, simulations of this type will be greatly improved.

But a deeper source of variation may be rooted in unexplored aspects of the ecology and natural history of each system that directly affect specific variables in the model. For example, in populations with high density or with a short and intense breeding season, reproductive activity expenditure can detract from the production budget (Anderson and Karasov, 1988) and the 11 *S. undulatus* study populations differ greatly in density (see sources in Table 1). This argues for estimating season-specific activity scopes (the fractional increase in metabolic rate above resting due to activity) for each site in order to correct the total maintenance expenditure. As another example, if the predation environments vary among sites, constraints may be placed on activity and thermoregulation that could go either way depending on the nature of the predator-prey interaction (e.g., high T_b selection to maximize escape probability, or low T_b due to selection of cool refuge microhabitats to reduce predator exposure). Additionally, high predation rates may select directly on energy allocation phenotypes by affecting age at maturity and age-specific reproductive effort (Stearns, 1976; Dunham *et al.*, 1988a). Finally, there could be operative constraints due to phylogeny which could elicit complex associations among model parameters among sites, despite the lack of an overall effect of phylogeny in a simple test by Dunham *et al.* (1988a). There is an obvious need for higher resolution in such analyses.

SUGGESTIONS FOR ADVANCED MODELS

In previous sections, we highlighted several areas where simplifying assumptions

used by the microclimate and physiological models deviated from biologically realistic levels of complexity. This section explores three such areas and presents ways in which the model presented above could be improved. We address how to incorporate biologically realistic levels of (A) thermal microclimate heterogeneity, (B) digestive performance, and (C) optimal allocation of time and resource to maximize fitness.

Spatio-temporal thermal heterogeneity and activity constraints

The microclimate model presented above uses an extremely simplified abstraction of the thermal environment to determine daily and seasonal constraints on activity and T_b selection. Increased metabolic and feeding rates associated with activity are viewed as step functions varying between 0, for inactivity, and some maximum during activity, for which the edges of these steps correspond to variation in the ranges of available T_s (see Fig. 4). However, several previous researchers (e.g., Waldschmidt and Tracy, 1983; Tracy and Christian, 1986; Grant, 1990; Grant and Dunham, 1988, 1990) have emphasized the importance of using the actual distribution of available thermal microclimates to delineate constraints on individual activity and home range use. Further, according to results in Grant (1990), the actual shape of the $T_s(t)$ distribution may directly influence the cost/benefit economics of lizard T_b selection during activity.

According to data from continuous observations of free-ranging *Sceloporus merriami* from the Grapevine Hills in Big Bend National Park, Texas (Grant and Dunham, 1988), individual activity rates (movements, feeding and social displays) during the morning activity period increased and decreased much more smoothly than do step functions. These authors concluded that the timing of peak activity rates as well as random microclimate use coincided with the time at which an indirect measure of the average available T_s equalled the mean selected T_b (calculated over all times in the morning). Subsequent work by Grant and Dunham (1990) greatly improved the resolution of the thermal environment in this system (by using arrays of hollow-body

painted models of *S. merriami*) and provides a direct estimate of the distribution of available T_s for reanalysis here.

In Figure 7 (upper panel) is plotted the fraction of model temperatures, T_s , within the interval 26.0°–36.5°C which encloses 95% of all T_b data from active lizards on cloudless summer days in the Grapevine Hills, and is a measure of the range of acceptable temperatures for active lizards under these conditions at this site (modified from Grant and Dunham, 1990). This figure indicates that by about 1000 hr almost 100% of the habitat is thermally amicable to these lizards, whereas, before 900 hr and after 1200 hr less than about 25% of the habitat is suitable for activity. Overlain on this figure are the average rates of individual movements (solid symbols, modified from Grant and Dunham, 1988), from which it is apparent that the temporal pattern of natural movement rates are poorly described by any step function as required by the model. Instead, movement activity shows more of a sinusoidal relation with time enclosing and in phase with the T_s availability curve. This suggests that the activity scope (=the ratio of active to inactive metabolic rate) should be a function of the distribution of available T_s within specified temperature bounds, i.e., when few microclimates exhibit acceptable T_s for activity, lizard activity scopes will be low, whereas when most microclimate T_s are suitable for activity, scopes will be maximal.

A similar result holds between the observed feeding rates and the distribution of T_s within the interval 26.0°–36.5°C (Fig. 7, lower panel), and somewhat surprisingly, the relationship is linear ($R^2 = 0.841$, $P < 0.01$). This shows that individual feeding strike rates by these wait-ambush arthropod predators can be accurately predicted by estimating spatio-temporal thermal heterogeneity. The explanation for the high degree of linearity in this relation may be as much, if not more, related to thermal environmental constraints on arthropod activity rates than to lizard thermoregulatory and prey capture strategies; however, data on this are lacking.

The above results clearly suggest that any useful macroclimatic model to predict

activity and food consumption constraints, must at least attempt to simulate these constraints at biologically realistic levels of complexity. One way to accomplish this, is to repeat the microclimate model numerous times for the same global site conditions but using randomly determined local perch and lizard body orientations. Each iteration would result in the $T_e(t)$ curve for one perch over a 24 hr period, and repeated iterations enable calculation of the distribution of available temperatures for the initial assumed topography (i.e., source distribution for perch orientations). Figure 8 (upper panel) illustrates the results from 40 simulations using randomly determined perch locations and lizard orientations on a hemispherical rock in mid-summer. These data may be used to calculate the fraction of available microclimates and infer activity constraints as a function of time of day for any hypothetical activity temperature range (Fig. 8, lower panel). These calculations can be used to model time dependent activity scopes and foraging rates more realistically, and examine the impact of differences in patterns of movement rate and foraging mode on energy budget sizes among populations or species.

Batch processing of ingested food

Recent work by Penry and Jumars (1986, 1987) has demonstrated the utility of chemical reactor theory in modeling the reaction kinetics in animal guts. In this view, a gut can be modeled as a continuous flow through reactor (for animals that feed more or less continuously as with many filter feeders and herbivorous mammals), or as a batch reactor (for animals that feed in discrete pulses such as many wait-ambush carnivores). These models specify the reaction kinetics, i.e., the rate equations relating ingested food to assimilable products, and simulate the steady state or transient mass balance for the gut. Variation in input parameters (e.g., morphology, physiology or feeding behavior) may provide insights into gut design constraints and identify critical variables affecting optimal gut function (Sibly, 1981; Taghon, 1981; Taghon and Jumars, 1984; Troyer, 1984; Penry and Jumars, 1987).

Since ectothermic lizard activity and

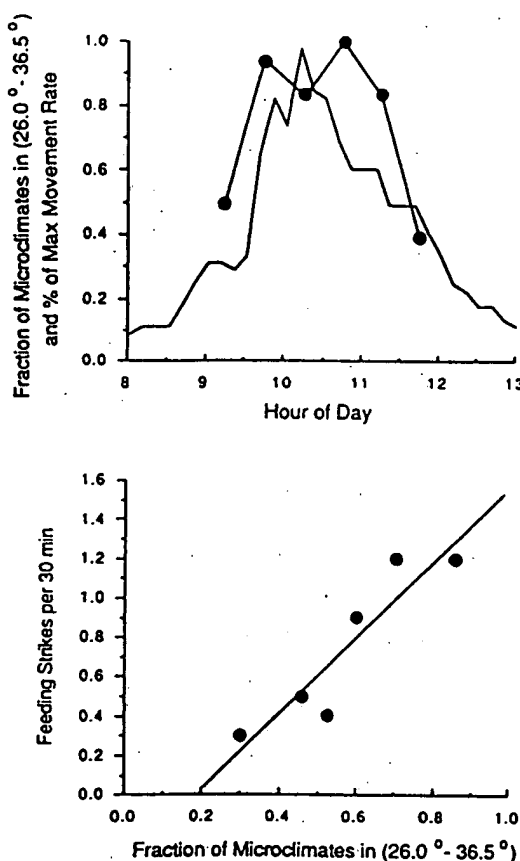


FIG. 7. UPPER PANEL: The fraction of microclimate temperatures within the interval (26.0°–36.5°) available to *Sceloporus merriami* for a typical mid-summer day in the Grapevine Hills, Big Bend, Texas. This interval encloses 95% of all body temperatures for these lizards at this site. Superimposed on this plot are the reanalyzed data on individual movement rates from continuous observations of free-ranging *S. merriami* (solid points, Grant and Dunham, 1988). These data are depicted as “% of maximal rate” in order to use the same scale as the microclimate fraction data. LOWER PANEL: The number of feeding strikes per 30 min by free-ranging *S. merriami* (from Grant and Dunham, 1988) is linearly correlated with the fraction of available microclimate temperatures within the interval (26.0°–36.5°). Both panels indicate that temporally variable feeding rates and activity scopes need to be included in macroclimatic constraint/energy budget models.

feeding rates are fairly discrete, depending on the temporal pattern of thermal microclimate availability (e.g., see the previous section and Fig. 7), we suggest that a batch reactor model may provide an adequate representation of lizard gut functioning. Such

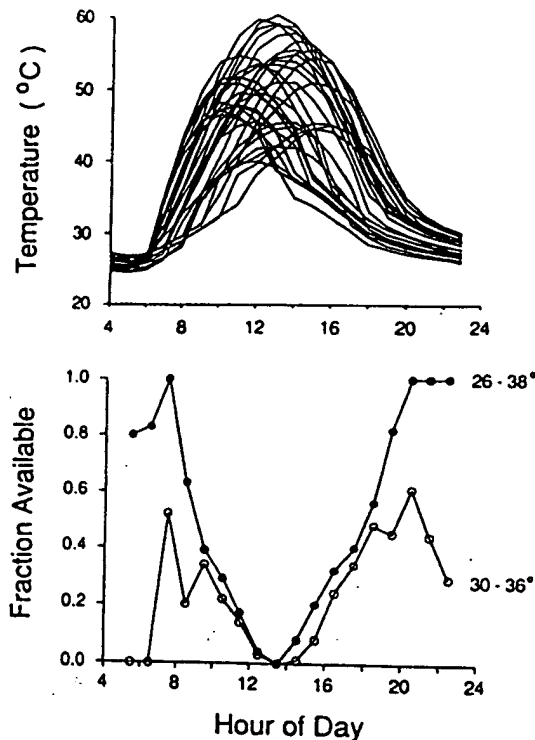


FIG. 8. UPPER PANEL: Simulated microclimate temperatures for 40 randomly oriented substrate surfaces from repeated iterations of the microclimate program. Each orientation was randomly selected from a point on the surface of a fictitious hemispherical rock; however, any other source distribution, *i.e.*, rock shape, may be used. LOWER PANEL: The fraction of simulated microclimate temperatures available to a hypothetical lizard within two typical body temperature intervals (26°–38°, solid points, and 30°–36°, open points). We based these fractions on 120 calls to the microclimate program (the first 40 of which are shown in the upper panel).

a model is needed to more realistically incorporate thermal constraints on resource processing capacity in any macroclimate constraint/energy budget simulation by allowing for digestion and assimilation to occur during times subsequent to consumption and at rates determined by the T_b at these later times (whether or not the lizard is active). Thus, a hypothetical lizard that has recently emerged with a low T_b may overfeed relative to its steady state ingestion rate at that T_b , and process these resources later in the day. On the other hand, if inactivity T_b is too low for complete gut clearance during the inactive period, the lizard's

consumption rate upon emergence for activity will be appropriately reduced.

We have developed a simple model for batch processing of ingested food based on the general formulation in Penry and Jumars (1987) and using the specific digestive performance relations derived for *Sceloporus undulatus* and presented in Appendix A. The model assumes that during each hour of activity the lizard (a) thermoregulates perfectly (constant T_b), (b) ingests enough food to completely fill its gut (its energy budget is limited by its food processing capacity), (c) digests this food at an hourly rate of $1/24$ of the daily rate estimated in lab at the same T_b (digestion rate is linear in time), and (d) metabolizes energy at a rate equal to the sum of its resting and activity rates as well as the cost of digestion. Also, during inactivity, the lizard does not feed and its hourly metabolic rate equals its resting rate plus the cost of digesting the food remaining in its gut, both of which are calculated for the inactivity cave T_b . A detailed explanation of this simulation is presented in Appendix B.

Results for several sensitivity analyses appear in Figure 9, each panel of which shows the cumulative energy budget size for the same set of default input parameters (upper curve) and the rate of energy accumulation due to a change in one of these parameters (lower curve). Note the decrease in the predicted energy budget size due to either lowering inactivity T_b (Panel A) or activity T_b (Panel B). These result from an increase in the food passage time and a concomitant drop in the hourly rate of digestion associated with lower T_b , and suggest that fed lizards should select warmer T_b s. This is consistent with numerous lab studies demonstrating higher T_b regulation after feeding by reptiles (reviewed in Waldschmidt *et al.*, 1987) as well as with field studies that suggest sleeping site thermal microclimate selection by lizards may be related to nighttime digestion requirements (Christian *et al.*, 1984; Huey *et al.*, 1989).

Panel (C) illustrates the sensitivity of the energy budget size to an increase in activity rate (a 10% increase in activity scope produced a 25% drop in the rate of energy accumulation). This difference in scope is prob-

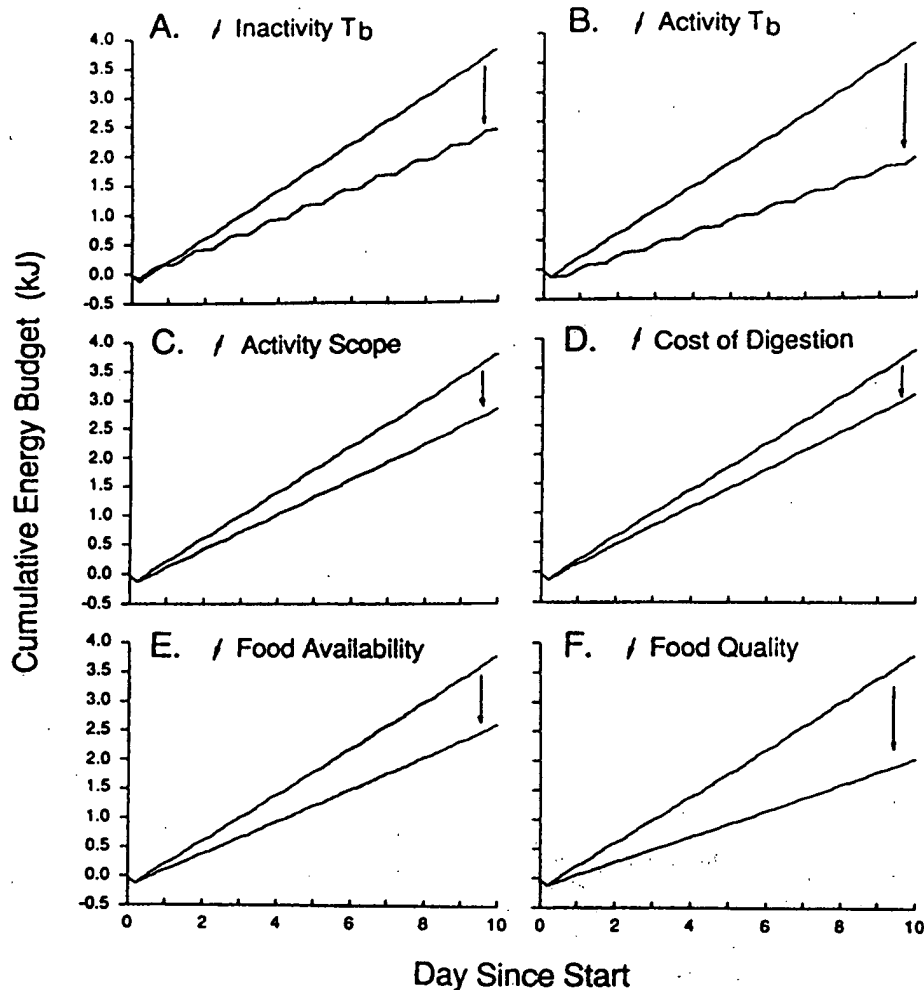


FIG. 9. Predicted cumulative energy budget size (kJ), for several sets of initial parameters according to a simple batch processing model (see Appendix B). Each panel shows the effect of a change in one of the driving variables (lower curve) relative to the amount of energy accumulated for a default parameter set (same upper curve in each panel) for which the hypothetical lizard was active for 12 hr at $T_b = 36^\circ\text{C}$, activity scope = 1.5, and was inactive for 12 hr at $T_b = 32^\circ\text{C}$ (see Appendix B for other defaults). PANEL A: the lower curve is for a lower inactivity T_b by 6°C to 26°C . PANEL B: the lower curve is for a lower activity T_b by 4°C to 32°C . PANEL C: the lower curve shows a 10% increase in activity scope to 1.65. PANEL D: the lower curve shows a 10% increase in the cost of digestion to 0.85 (see "constant" in eq. B1, Appendix B). PANEL E: the lower curve shows a 10% decrease in food availability to 90% of the *ad lib.* feeding rate. PANEL F: the lower curve shows a 10% decrease in food energy density to 23,040 J/g dry wt.

ably an underestimate of that exhibited by some lizards (Waldschmidt *et al.*, 1987). According to the model, higher scopes quickly lead to zero or negative net accumulation (not shown), which is consistent with field observations of reproductively active male lizards (Anderson and Karasov, 1988; Grant and Dunham, 1990).

Panel (D) shows that an across the board increase in the cost of digestion by 10% (e.g., if consumed food were more difficult to digest, or if our guess for the "constant" in eq. B1, Appendix B were too low) effects a 10% decrease in the rate of energy accumulation. Panels (E) and (F) show that decreases in estimated food availability or

food energy density, respectively, also dramatically affect the energy budget.

The extreme sensitivity of our energy budget model to variation in input parameters as shown in Figure 9 argues strongly for directly estimating these parameters under field conditions for the particular lizards of interest. But more importantly, these model parameters describe important physiological and behavioral characters of the study lizards and may provide useful bases for comparison among populations in different thermal and food resource environments. Formulating appropriately resolved batch processing models would more realistically mimic the phenotypic processes of energy accumulation by individuals in different populations. This would provide necessary optimality criteria to generate hypotheses for the evolution of thermal physiology and thermoregulatory behavior subject to environmental thermal and resource availability constraints. We develop this idea further in the next section.

Behavioral optimization

A substantial short-coming of our present macroclimatic constraint/energy budget model is the simplistic set of responses allowed by the hypothetical ectotherm to variation in simulated resource and thermal environmental constraints (see Fig. 4). But, according to the schematic in Figure 1, organismal fitness should involve maximizing the expected sum of current and future fecundity. Toward this end, our model must be modified to include explicit predictions about how lizards should optimally acquire and process resources on a daily basis (short term foraging strategy) and optimally allocate assimilated resource over a breeding season and/or lifetime (longer term life history strategy). The problem is one of reducing a diverse set of environmental constraints and risks associated with possible "actions" into a single currency, *e.g.*, fitness, and formulating an amalgamated cost/benefit function that determines the time and energy allocation phenotype by the hypothetically optimizing organism (McCleery, 1978; McNamara and Houston, 1986; Dunham *et al.*, 1989). Numerous studies have used diverse optimization

techniques to generate hypotheses about life historical time and energy allocation including exact solutions using optimal control (King and Roughgarden, 1982; Iwasa and Roughgarden, 1984; Werner, 1986; Hom, 1988), numerical approximations such as the quasi-Newton method (Taylor and Gabriel, 1992), or stochastic dynamic programming (McNamara and Houston, 1986; Mangel and Clark, 1988; Hom *et al.*, 1990).

In this section we describe a simple model of optimal time allocation by an hypothetical lizard maximizing its long term survival and energy budget size in order to demonstrate the utility and ease of inclusion of optimality models in our macroclimatic constraint/energy budget modeling. We use the methods of stochastic dynamic programming since according to Hom *et al.* (1990) these methods are heavily founded on ecological specifics of the study system and return explicit and testable predictions. In our model, our hypothetical lizard may be either active or inactive depending on its body energy reserves, resource and thermal environmental characters, and risk of mortality due to foraging. As organized by Mangel and Clark (1988), our model has five essential components. First, the "state space" is the energy state, x , of the lizard at time t . Second, the "constraint set" we use is an interval constraint, *i.e.*, x must be in $[0, \max x]$. Third, the "strategy set" relates simply that the lizard must be either active and foraging or inactive (at predetermined activity and inactivity $T_{a,s}$, respectively). Fourth, the state dynamics relate to how the energy state and probability of mortality are affected by being active *vs.* inactive. In our model, the lizard's energy state is decremented each time interval due to its resting metabolism (as a function of its T_b), and if it is active and foraging, the costs of these are also deducted. The lizard's energy state can only be increased by being active and foraging; however, predators may also be encountered during activity, but not inactivity. Food and predator encounters are expressed as probabilities which motivates the term "stochastic" to describe this type of state variable model. Lastly, the "optimization criterion" in our model is to choose to be active or inactive for each x and t .

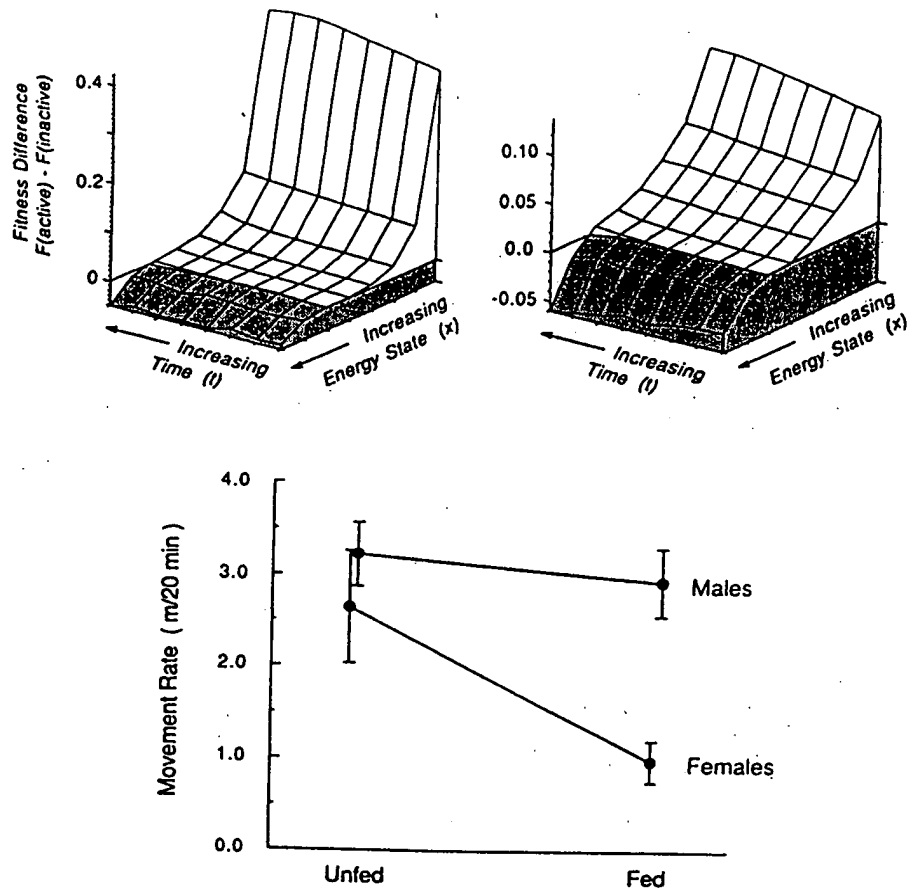


FIG. 10. UPPER PANEL: Typical response surfaces for the predicted fitness difference between being active vs. inactive for each energy state and time interval according to a simple stochastic dynamic model of optimal time allocation. We show results for low and high food availability (upper right and left, respectively, values for all input parameters are given in Appendix C). Generally, food stressed lizards should be active (positive Z-values), whereas well-fed lizards should be inactive (negative Z-values, shaded portion of the response surface). Variation in the shape of the response surface due to varying other input parameters (e.g., predation rate, metabolic expenditure, etc., see Appendix C) is qualitatively similar to that shown here (see text). LOWER PANEL: Individual activity rates (meters moved per 20 min, ± 1 SE) from continuous observations of supplementally fed male and female *Sceloporus merriami* in a population near Cuatro Ciénegas, México (Grant and Contreras-Arquieta, unpublished data). Rates for fed females were lower than for unfed females, but fed and unfed male movement rates did not differ.

depending on which choice simultaneously maximizes the probability of surviving as long as possible while attaining the greatest energy state after a long time. We present the equations and pseudocode for this simulation in Appendix C.

Figure 10 illustrates two representative response surfaces from our model of optimal time allocation (see Appendix C for parameter inputs for these simulations). Energy state and time are plotted in the hor-

izontal plane, and since there are only two possible choices in the "strategy set" (active or inactive), we plot the predicted fitness difference ($F_{\text{active}}(x, t, T) - F_{\text{inactive}}(x, t, T)$) along the Z-axis for each x and t . Positive Z-values indicate that activity is optimal, and negative Z-values (shaded portions in Fig. 10) indicate that inactivity is optimal. As can be seen in both response surfaces, the model predicts that lizards with low to moderate energy states should be active,

whereas energetically endowed lizards should be inactive to maximize their long term fitness.

The difference between response surfaces in Figure 10 is due to an increase in food availability (the parameter β in Appendix C) for which the fitness difference for being active increases greatly (note different scales of Z), but only for low energy states. We have conducted detailed analyses in other regions of this six-dimensional input parameter space, and the qualitative difference between response surfaces in Figure 10 is typical of variation in other input parameters. In general, there are often large differences in the predicted fitness values as well as some variation in where the cutoff for activity occurs among states in x ; however, all simulations were consistent with the result that energy state and activity level should vary inversely. Additionally, we have simulated predation during inactivity (such as by fossorially foraging snakes), and we have examined the effect of a risk of predation during any change from activity to inactivity (such as by wait-ambush snake predators near crevice openings [we thank A. Cannon for this model]), all of which support the qualitative prediction in Figure 10 that activity rates should be lowest for well fed lizards.

According to results from a field resource supplementation experiment, in which marked free-ranging *Sceloporus merriami* lizards were individually fed individual crickets, the activity rates of fed females were significantly lower than were the rates for control unfed females (Fig. 10, Grant and Contreras-Arquieta, unpublished data). Thus, female *S. merriami* appear to conform to the predictions of our optimal time allocation model. Note however, that the activity rates for fed and unfed males did not differ (there were no differences in the amount of food supplemented to treatment females and males). We interpret this difference to be indicative of the difference in reproductive strategies between the sexes for these highly social lizards. For male *S. merriami*, reproduction depends greatly on territorial acquisition and exclusion of competing males, as well as on spatial overlap,

encounters, and courtships with neighboring females (Ruby and Dunham, 1987). In contrast for females, the amount of her energy reserves will greatly determine her reproductive output (Dunham, 1981) which is consistent with an underlying assumption of the model that energy and predation constraints are sufficient to drive behavior. We suspect that the lack of concordance between the model predictions and male responses is because the assumptions of the model poorly described the fitness criteria for male reproduction which may be greatly affected by operative social/demographic constraints on male reproductive activity (Dunham *et al.*, 1989).

These results underscore the necessity of obtaining a detailed understanding of the natural history of the study system prior or parallel to any modeling attempt. But more importantly, constraints from the social/demographic environment dictated by requirements of mate acquisition in polygynous social systems can profoundly affect adult male behavior and must be included in behavioral optimization models. More advanced models must recognize that different sexes and ages may have different optimization criteria, and simultaneously include all relevant factors impinging on the daily behavioral and seasonal resource allocation phenotype from the biophysical, resource, social/demographic and predation environments (Dunham *et al.*, 1989).

CONCLUDING REMARKS :

The macroclimate constraint/energy budget model we describe relies on basic physical characters of microclimates and well-known biophysical and bioenergetic characters of lizards to delineate environmental constraints on individual activity, food consumption, and food processing capacity. We stress that this modeling can *only* predict the size of the energy budget available for allocation to growth, storage and reproduction in a life history and not how that resource should be allocated to maximize fitness (see Figs. 1 and 3). Therefore, models of this type should be used as a "front-end" to provide the bounding envi-

ronmental constraints on individual ectotherm energy budgets within which future models of optimal resource acquisition and allocation must operate. We advocate as have others (e.g., DeAngelis *et al.*, 1979; Huston *et al.*, 1988) that such "individual-based" models are an important tool to explore potential population and community level responses to macroclimatic variation. These formulations have the advantage of being extremely system-specific and thereby generate testable predictions about the mechanistic effects of interacting environmental constraints on, and the adaptive significance of, variation in individual life history characters (Dunham *et al.*, 1989).

According to many scenarios of climate change (COHMAP, 1988) the magnitudes of predicted changes in the driving macroclimatic characters (e.g., temperature, humidity, and cloud cover) are similar to presently existing differences among sites separated by only a few hundred meters in elevation or a few degrees in latitude. Therefore, results of interdisciplinary studies of present day patterns of covariation in environment and life history among geographically distinct populations may be extrapolated to generate hypotheses about individual and population level responses to climate change in a given location. However, such an extrapolation cannot be made without a thorough knowledge of the study organism and of the complexities of the interactions between individuals and their total environment (biophysical, resource, social/demographic and predation, Dunham *et al.*, 1989). An important lesson from numerous among-site comparisons of life history and environmental covariation (e.g., *Sceloporus merriami*, Grant and Dunham, 1990) is that individual responses to interacting environmental gradients may involve significant age, sex, site, and season interactions among life history characters.

The correlation between observed and predicted energy budget sizes among populations of *Sceloporus undulatus* (Fig. 6) suggests that our modeling efforts are on track; however, the limited resolution and relatively short duration of most of the comparable field studies as well as the lack of

data on geographical and seasonal variation in physiological ecology are significant impediments to modeling advances. Progress in this area requires a tremendous increase in the resolution, duration and number of population ecology studies in order to use broad intra- or interspecific comparisons to generate and assess hypotheses concerning the evolution of life histories as well as population responses to climate change. These studies must be interdisciplinary and include detailed physiological and biophysical modeling as well as estimates of constraints from the resource, predation and social/demographic environments. Such studies must also be of sufficient duration to elucidate the temporal dynamics of individual and environmental covariation (Nichols *et al.*, 1976) since critical life history characters such as growth, survival and reproduction tend not to be constant (e.g., Dunham, 1978, 1981) and in fact may exhibit adaptive plasticity (Caswell, 1983; Stearns, 1986; Newman, 1988). Finally, studies must include assessments of the genetic bases of individual responses to environment in order to model long-term evolutionary effects of climate change. An important aspect of using interpretations of present day geographic covariation in life history and environment (for which environments have undoubtedly differed for a very long time) to generate predictions about the effects of climate change within a location is to determine the time frame over which macroclimatic characters vary relative to organismal evolutionary response times. Controlled reciprocal transplant and common garden experiments are ideally suited to detect genetic effects and should be seen as a research priority despite their extremely time- and labor-intensive methods.

Clearly, long-term interdisciplinary databases will be crucial in the development and testing of advanced models that link macroclimate and individual autecology to population and community ecology, and we suspect that the data needed for testing these models are likely to exceed the capabilities of any individual laboratory in terms of labor, logistics, and required degree of spe-

cialization. An organized collaboration among research specialists is likely to be far more productive than any single generalist given the same resources. Therefore, we urge in this era of evaporating funding that interdisciplinary research should increase in priority as an important means to resist the potentially divisive effects of increased competition for ever-scarcer research support.

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APPENDIX A.

Equations used in the ectotherm physiological simulation.

Hourly Metabolic Expenditure, $= Q_{MET}$ (J/hr): The metabolic rate of an active lizard is assumed to be a constant fraction times its resting rate ($=$ activity scope, Bennett and Dawson, 1976; Congdon *et al.*, 1982). Resting metabolic rates for this simulation are obtained from a regression in Bennett and Dawson (1976):

$$Q_{MET} \text{ (J/hr)} = 20.2 \cdot 10^{0.038(T_b - 17.71)} \cdot \text{lizard mass}^{0.82} \cdot \text{activity scope (eq. A1)}$$

The coefficient preceding the first exponent assumes that the lizards are insectivorous (see Bennett and Dawson, 1976), and a value of 1.5 was selected for the "activity scope" which is appropriate for active iguanids (Congdon *et al.*, 1982).

Hourly Resource Accumulation, $= Q_{AVAIL}$ (J/hr): Maximal food consumption and assimilation rates were determined for a lizard as a function of T_b by estimating the steady state rates of ingestion and excretion (J/day) by lizards held at constant cage temperature and in either an *ad lib.* feeding regime or a regime at 50% of *ad lib.* (data and regressions from *Sceloporus undulatus*, see Waldschmidt, 1984; Waldschmidt *et al.*, 1986, 1987). These rates were then converted to hourly rates by dividing by 24 hr. Note that if the lizard is not active during a particular hour, then the value for Q_{AVAIL} is zero for that hour. The regression for the digestive efficiency as a $f(T_b)$ was obtained from arcsine square-root transformed values since these were proportions (Sokal and Rohlf, 1981). The generating equations are:

$$\text{max consumption rate (mg wet wt/g-day)} = -328.7 + 22.82 \cdot T_b - 0.320 \cdot T_b^2 \quad (\text{eq. A2})$$

$$\begin{aligned} \text{actual consumption rate (mg wet wt/hr)} \\ = \text{max consumption rate} \cdot \dots \\ \cdot \text{fraction of } ad \text{ lib. feeding} \cdot \dots \\ \cdot \text{lizard mass/24 hr} \end{aligned} \quad (\text{eq. A3})$$

$$\begin{aligned} \text{arcsin digestive efficiency} \\ = 85.34 - 0.50 \cdot T_b + \dots \\ + \begin{cases} 0 & \text{if frac. of } ad \text{ lib.} = 1.0 \\ 0.000074 \cdot T_b & \text{if frac. of } ad \text{ lib.} < 1.0 \end{cases} \end{aligned} \quad (\text{eq. A4})$$

$$\begin{aligned} \text{digestive efficiency} \\ = [\sin((\pi/180) \cdot \text{arcsin digestive efficiency})]^2 \end{aligned} \quad (\text{eq. A5})$$

$$\begin{aligned} Q_{AVAIL} \text{ (J/hr)} = \text{actual consumption rate} \cdot \dots \\ \cdot (1 - \text{food percent water}) \cdot \dots \\ \cdot \text{digestive efficiency} \cdot \dots \\ \cdot \text{food energy density} \end{aligned} \quad (\text{eq. A6})$$

In eq. A3, the "fraction of *ad lib.* feeding" ranges between 1.0 for *ad lib.* feeding to 0 for no feeding. In eq. A6, we assigned values of 0.75 for "food percent water" and 25,600 J/g dry weight for "food energy density" according to Waldschmidt *et al.* (1986).

APPENDIX B.

Equations used in the batch processing simulation

Our batch processing resource assimilation model uses the specific digestive performance relations derived for *Sceloporus undulatus* (see Appendix A) to find the amount of food ingested and assimilated per hour for a user defined 24 hour cycle of T_b and activity, and then simply sums the total assimilated (which was defined earlier as the discretionary resource, $\equiv \text{DER}$) over all of the hours during a 10 day period.

In addition to assumptions mentioned in the text (i.e., step functions in activity rate and T_b selection in time, and food consumption constrained only by gut volume), we must also assume some relation for the cost of digestion, or the specific dynamic action ($\equiv Q_{SDA}$). According to Waldschmidt *et al.* (1987), Q_{SDA} in *S. undulatus* varies with the amount of food in the gut as well as with T_b , and can be as great as the resting metabolic rate (i.e., $1.0 \cdot Q_{MET}$) for lizards with full guts. In the absence of any quantitative basis, we assumed that Q_{SDA} co-varied linearly with Q_{MET} (eq. A1), and was proportional to the ratio of the amount of food presently in the gut divided by the maximal gut capacity (found by differentiating eq. A2 to get the optimal T_b of 35.7°, and using this value in eq. A2). Thus we assumed,

$$Q_{SDA} = \text{constant} \cdot (\text{food volume in gut} \div \dots \div \text{max gut capacity}) \cdot Q_{MET} \quad (\text{eq. B1})$$

We chose a value for the constant in this equation of 0.75 which is within the range 0.5–1.0 for *S. undulatus* (Waldschmidt *et al.*, 1987, see their Table V, p. 573). We emphasize that data are critically lacking on the cost of digestion in lizards.

To estimate the hourly assimilation rate we per-

formed a polynomial regression of lab data on food passage rate for *S. undulatus* in Waldschmidt (1984, $R^2 = 0.987$):

$$\begin{aligned} \text{passage rate (days)} = 102.891 - 8.6812 \cdot T_b + \dots \\ + 0.251568 \cdot T_b^2 - \dots \\ - 0.00247528 \cdot T_b^3 \end{aligned} \quad (\text{eq. B2})$$

and we assumed that the hourly passage rate was simply $1/24$ of the daily rate. Thus, the hourly assimilation rate is given by:

$$\begin{aligned} \text{assimilation rate} \\ = \frac{\text{digestive efficiency (from eq. A5)}}{\text{passage rate} \cdot 24 \text{ hours}} \end{aligned} \quad (\text{eq. B3})$$

Below we present the pseudocode for this model and we encourage readers to construct their own models using other versions of the generating equations specific to other taxa of interest:

```
begin simulation
begin day
for each hour of day do
  -if active then get activity tb and metabolic
    scope and fill gut volume, V, to capacity
    (eq. A1);
  -else if inactive get inactivity tb and set met-
    abolic scope equal to 1.0;
  -calculate the hourly assimilation rate (eq. B3);
  -calculate the volume of food digested during
    the hour, dV, from the product of the assim-
    ilation rate and the volume of food in the
    gut, V;
  -calculate the amount of energy in dV,  $\equiv Q_{AVAIL}$ 
    (J/hr), using  $Q_{AVAIL} = dV \cdot (1 - \text{food percent
    water}) \cdot \text{food energy density}$  (modified from
    eq. A6, and see Appendix A for coefficients)
  -calculate the metabolic rate,  $Q_{MET}$  (eq. A1),
    and the cost of digestion,  $Q_{SDA}$  (eq. B1);
  -increment the energy budget, DER, by +
     $Q_{AVAIL} - Q_{MET} - Q_{SDA}$ ;
  -decrement gut volume by dV;
end of hour and increment to next hour;
end of day and increment to next day;
end of simulation;
```

APPENDIX C.

Equations used in the stochastic dynamic model of optimal time allocation to activity or inactivity by a lizard

This section describes the specifics of our particular model and omits most of the generalities of the methods. For readers who are interested in a general description of the methods of stochastic dynamic programming, we highly recommend an excellent book by Mangel and Clark (1988). In our model, the lizard's energy state is decremented each time interval due to its total metabolic cost of being active, $Q_{MET}(\text{active})$, or inactive, $Q_{MET}(\text{inactive})$, according to equation A1 for specified activity and inactivity T_b s. Further, the lizard's energy state can only be increased by being active, during which food of value α is encountered with probability β , and predators are encountered with probability Γ (which instantly reduces state and fitness

to zero). Thus, if the lizard is active, one of three outcomes is possible for its state at time $t + 1$ (eq. C1):

$$x(t + 1) = \begin{cases} x(t) - Q_{\text{MET}}(\text{active}) + \alpha & \text{w/ probability } \beta \cdot (1 - \Gamma) \\ x(t) - Q_{\text{MET}}(\text{inactive}) & \text{w/ probability } (1 - \beta) \cdot (1 - \Gamma) \\ 0 & \text{w/ probability } \Gamma \end{cases}$$

but, if it is inactive, only one outcome is possible:

$$x(t + 1) = x(t) - Q_{\text{MET}}(\text{inactive}) \quad (\text{eq. C2})$$

To encapsulate the optimality criterion, we form the dynamic programming equation to find $F_{\text{active}}(x, t, T)$ and $F_{\text{inactive}}(x, t, T)$, which are the fitness functions for active or inactive lizards, respectively, with state x over the interval t to T , and assuming behavior is optimal for all times thereafter, *i.e.*, between $t + 1$ and T , (see Mangel and Clark, 1988, for a highly readable presentation of the general formulation of the dynamic programming equation) (eq. C3):

$$F_{\text{active}}(x, t, T) = [(1 - \Gamma) \cdot \beta \cdot F_1(x(t + 1)) + (1 - \beta) \cdot \dots \cdot F_2(x(t + 1))]$$

$$F_{\text{inactive}}(x, t, T) = F_2(x(t + 1))$$

Where, $F_1(x(t + 1))$ and $F_2(x(t + 1))$ = the fitness of the lizard with state $x(t + 1)$ in the next time interval assuming that it was active and successfully found food, or was active and did not find food, respectively, according to eq. C1. And, $F_2(x(t + 1))$ = the fitness of the lizard with state $x(t + 1)$ in the next time interval assuming that it was inactive, according to eq. C2. Whether the lizard should be active or not depends on the larger of the two fitnesses, $F_{\text{active}}(x, t, T)$ vs. $F_{\text{inactive}}(x, t, T)$.

Note that these are recursive equations where the fitnesses for choices at time t depend on the fitnesses at time $t + 1$, thus, these equations can be solved by specifying the ending state vs. fitness distribution (also

called the "terminal fitness function") and iterating backwards in time. For our simulation we chose a linear terminal fitness function ($F[x, T, T] = x/\text{maximum } x$) as one way to meet our "optimization criterion" that the lizard should seek the greatest long-term energy state possible during its foraging.

For the simulation in Figure 10, we choose a 10 min interval as our unit of time and 1 J as our unit of energy state x , ranging from 0 to 60 J. These selections were constrained by our computing capacity; however, we note that much leeway exists in the appropriate selection of time and state resolution since we are interested in the qualitative pattern of response (*i.e.*, should the lizard be active or inactive) and not the absolute fitness predictions. We selected activity and inactivity T_s of 26° and 36°C, an activity scope of 2.0 (1.5 for activity + 0.5 for food processing), a value of 0.05 for predation risk Γ , and a value of 20 J for net food energy content α . Lastly, to show the effect on the predicted response surface of increased food availability, we used food encounter probabilities, β s, of 0.75 (Fig. 10, upper left) and 0.50 (Fig. 10, upper right).

Below is the pseudocode for this simulation:

```
begin simulation
  initialize linear terminal fitness array,
  set fitness for state  $x$  {from 0 to max  $x$ }
    =  $x/\text{max } x$ 
  initialize the time counter to its maximal value,  $T$ 
  repeat iterating backwards in time
    for each energy state from 0 to max  $x$  do
      compute the changes in energy state  $x$  due to all
        possible outcomes for activity and inactivity
        (eq. C1 and eq. C2)
      compute the fitness functions to find the expected
        fitness for choosing to be active or inactive
        (eq. C3)
      if  $F_{\text{active}}(x, t, T) > F_{\text{inactive}}(x, t, T)$  then be active,
        otherwise be inactive for  $x$  and  $t$ 
      decrement the time counter
    return to repeat again and quit after a long time into
      the past
  end simulation.
```

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- ☐ **GRAY SCALE DOCUMENTS**
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